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Abstract: Humans stand out among primates and other mammals in reaching adult-level foraging skills very late in development, well after the onset of reproduction. The aim of this paper is to place this unusual human skill development into a broader comparative context. Among birds and mammals in general, duration of immaturity, indexed by age at first reproduction (AFR), and adult brain size have undergone correlated evolution. This pattern is consistent with two causal processes: AFR is either limited by the time needed to learn adult-level skills (needing to learn) or by the energy needed to grow brain and body to full size (energetic constraints). We tested predictions arising from these two hypotheses with data retrieved from the published literature for 57 mammal and bird species. First, most mammals reach adult-level foraging skills well before the developmental period is completed, implying that energy constraints determine the age at first reproduction, whereas most birds reach adult-level foraging skills around the time of maturity, suggesting time needed for skill acquisition determines the onset of reproduction. Second, within mammals we found that with increasing niche complexity, the age of adult-level skill competence moves closer to the age at first reproduction. Third, when looking at how adult-level skills can be reached later, we found that gregariousness, slow conservative development and post-weaning provisioning allow mammals to reach their skills later. Finally, in species with intense sharing of resources (such as cooperative hunters) competence in foraging skills may even reach peak values after age of first reproduction. We conclude that the human pattern of skill acquisition could arise because our hominin ancestors added cooperative breeding and hunting to the slow development they had as great apes with increasingly complex niches. This result provides a broad biological foundation for the embodied capital model.

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How to explain the unusually late age at skill competence among humans?

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Abstract

Humans stand out among primates and other mammals in reaching adult-level foraging skills very late in development, well after the onset of reproduction. The aim of this paper is to place this unusual human skill development into a broader comparative context. Among birds and mammals in general, duration of immaturity, indexed by age at first reproduction (AFR), and adult brain size have undergone correlated evolution. This pattern is consistent with two causal processes: AFR is either limited by the time needed to learn adult-level skills (*needing to learn*) or by the energy needed to grow brain and body to full size (*energetic constraints*). We tested predictions arising from these two hypotheses with data retrieved from the published literature for 57 mammal and bird species. First, most mammals reach adult-level foraging skills well before the developmental period is completed, implying that energy constraints determine the age at first reproduction, whereas most birds reach adult-level foraging skills around the time of maturity, suggesting time needed for skill acquisition determines the onset of reproduction. Second, within mammals we found that with increasing niche complexity, the age of adult-level skill competence creeps up toward the age at first reproduction. Third, when looking at how adult-level skills can be reached later, we found that gregariousness, slow conservative development and post-weaning provisioning allow mammals to reach their skills later. Finally, in species with intense sharing of resources (such as cooperative hunters) competence in foraging skills may even reach peak values after age of first reproduction. We conclude that the human pattern of skill acquisition could arise because our hominin ancestors added cooperative hunting and resource pooling to the slow development they had as great apes with increasingly complex niches. This result provides a broad biological foundation for the embodied capital model.

Keywords: skill learning; development; niche complexity; embodied capital; cooperative hunting; provisioning

1 Introduction

Human children take many years to learn how to forage efficiently. Among human foragers, women reach peak foraging efficiency in their mid-20s, i.e. well after the age at first reproduction of around 19 for women, whereas men reach theirs even later, in their 30s or 40s (Hill and Kaplan, 1999; Gurven et al., 2006; Kaplan et al., 2007). Some components, for instance strength and athleticism (e.g. ability to hit a target: Blurton-Jones and Marlowe, 2002), reach their peak values soon after AFR, but human foraging, especially hunting, requires experience-based knowledge of detailed processing techniques and prey behavior. Moreover, there is no reason to assume that hunters and gatherers do not maximize their returns during foraging trips, supporting the interpretation that the experience required for successful gathering, and hunting in particular, takes years to accumulate. The *embodied capital hypothesis* (Hill and Kaplan 1999; Kaplan et al., 2000, 2007) argues that the late acquisition of peak foraging efficiency in humans reflects the coevolution of our complex foraging niche and our unique provisioning system. Thus, the exceptionally late acquisition of efficient skills can be linked to the skill intensity of the foraging niche, and is made possible by massive intergenerational transfers of food from adults to immatures.

Humans are therefore unusual in two distinct ways (Hill and Kaplan, 1999). First, we reach adult-level skill competence well after weaning, whereas most mammals do so around or soon after weaning (see also Janson and van Schaik, 1993). This raises the general question in which conditions selection favors or allows an increase in the age at which adult-level skills are reached relative to the timing of weaning. Second, we reach skill competence not just late, but well beyond the age at first reproduction. This is unexpected, because animals that are less efficient than reproducing adults are not expected to be able to sustain the additional effort of reproduction. Almost certainly, therefore, skill acquisition after the onset of reproduction requires extensive food sharing or net provisioning, which raises the broader question about the role of provisioning in the evolution of highly complex foraging niches.

The aim of this paper is to place human skill development into a broader comparative context, by examining whether variation in the timing of the acquisition of adult-level skills across a broad array of birds and mammals is caused by (i) the time needed to learn the skills, or (ii) the energy allocated (and thus time needed) to complete full somatic growth and differentiation. Once we have identified the conditions in which time needed to learn skills limit the attainment of maturity, we can explore whether the human pattern arose through a process or a combination of processes also found in other taxa, or instead reflects processes unique to human evolution. This comparative analysis will allow us to dissect the embodied capital hypothesis into two major components, one focusing on the coevolution between the complexity of foraging skills (and thus brain size) and life history, and the other on the role of resource pooling and provisioning.

1 In this paper, we therefore first ask for birds and mammals in general which factors determine
2 the age at which adult-level foraging skills are reached. We will assume that this point is reached before,
3 or at most around, the age at which reproduction begins, but will later discuss exceptions to this general
4 rule as well. For birds and mammals (Figure 1), age at first reproduction (denoted here as AFR) is
5 determined by brain size, and not, as might be expected, by body size; humans follow the primate trend
6 in this respect. However, this correlation is consistent with two distinct processes. First, AFR may be set
7 by the time needed to grow and differentiate the adult brain, which develops before full body size is
8 achieved. Second, AFR may be set by the time to learn the requisite skills. In other words, we can ask
9 whether it is time (skill learning) or energy (growth and differentiation) that generally limits the duration
10 of the immature period among birds and mammals. We can differentiate between these two
11 possibilities by asking, within any given species, at what age adult-level foraging skills (denoted here as
12 Age at Skill Competence, or ASC) are reached relative to the onset of reproduction (AFR). The focus is on
13 ecological skills, in particular foraging, because they are known to be directly related to fitness
14 (Stephens and Krebs, 1986), whereas social skills, including parenting, are best practiced while
15 performing them, and are not improved by delaying reproduction (Silk, 1999). Once we have a general
16 answer, we can explore the third possibility: that ASC is reached after AFR. We expect this to depend on
17 provisioning or food sharing among adults, because weaned mammals or fledged birds, let alone
18 reproducing ones, must under normal conditions be able to sustain themselves.

19 The *needing to learn hypothesis* (Ross and Jones, 1999) claims that the interspecific correlation
20 between brain size and AFR arises because of the increasingly long time larger-brained species need to
21 acquire skills and knowledge essential for adult survival and reproduction (rather than time needed to
22 reach the requisite size and strength). This is so because some of the essential skills are expected to
23 develop gradually during immaturity. Thus, as the maturing individual must learn more and more and
24 complex skills, one expects AFR to go up accordingly (Ross and Jones, 1999). The same idea has often
25 been invoked for humans (Dobzhansky, 1962), but it alone cannot explain why humans reach ASC *well*
26 *after reaching* AFR rather than at the same time as AFR. This perspective is consistent with the insight
27 that brain development is an interactive process, where brain maturation requires constructive learning,
28 which inevitably takes time (Quartz and Sejnowski, 1997).

29 The needing to learn hypothesis was originally developed for birds. Probably due to intensive
30 provisioning by both parents, altricial bird nestlings grow very rapidly, much faster than even
31 provisioned mammal offspring, and reach adult body size before or soon after fledging (Ricklefs, 1968;
32 Guo et al., 2010), perhaps because reaching adult size and locomotor competence is important to avoid
33 predation (Lack, 1968). Nonetheless, in many species the onset of breeding is delayed for months or
34 even years (e.g. Morrison et al., 1978). Ashmole (1968) first proposed that immature birds lack

important foraging skills for their maintenance. A variety of studies have since confirmed this proposal (reviewed by Marchetti and Price, 1989).

We can visualize the hypothesis and its main prediction as follows (Fig. 2.a). Adult body size is reached before ASC. Thus, AFR is limited by the time to reach ASC. This is expected where there is a combination of high somatic growth rate, as in birds, and a skill-intense foraging niche (in either birds or mammals).

Among mammals in general, support for this idea appears to be limited (Janson and van Schaik, 1993; Deaner et al., 2003), because they are generally thought to reach adult-level skills well before reaching maturity, i.e. $ASC \ll AFR$. With respect to nonhuman primates, empirical studies have been inconclusive: although some provide support for the needing to learn hypothesis (Johnson and Bock, 2004, Gunst et al., 2010) most do not (Janson and van Schaik, 1993; Stone et al., 2006). Most mammal species must be self-supporting right after the age of weaning, as there is no post-weaning provisioning of immatures. Consequently, they must have enough skills to be at least self-sufficient, although this does not necessarily mean that these juveniles have reached adult-level skill competence (Charnov, 2001), because they are still smaller than adult and non-reproducing. The fact that they still keep growing until shortly before the onset of reproduction (Charnov, 2001) strongly suggests that skill competence is reached earlier. This argument implies that the timing of maturity in most mammals is limited by the time needed to reach adult body size.

This second explanation for the correlation between brain size and development time stresses the *energetic constraints* of development. We expect that full growth and differentiation of the brain must necessarily precede that of the body to guarantee a functional organism, which is indeed observed (Sacher and Staffeldt, 1974). The unusually high energy costs of brain tissue (Rolfe & Brown, 1997) accounts for the slower development in large-brained species, especially among monotokous precocial mammals that cannot reduce litter size (the expensive brain framework: Barrickman et al., 2008; Isler and van Schaik, 2009a). We can visualize this hypothesis and prediction as follows. Age at adult-level skill competence (ASC) is reached before adult body size, and consequently the energy allocated to (and thus time needed) to develop brain and body determines age at first reproduction (AFR) (Fig. 2.b). This pattern is expected where the skill intensity of the niche is low relative to development rate.

The third possibility is where adult level skills are reached well after age at first reproduction (Fig. 2.c). This implies a complex foraging niche, because otherwise AFR would be reached sooner, and thus assumes that time needed to learn acts as the constraint on reaching AFR. But in addition it must assume some form of food sharing among adults (Kaplan et al., 2000), because otherwise reproduction could not be supported. This is the pattern consistent with the embodied capital hypothesis.

Predictions tested

This analysis of the factors limiting the age at which sexual maturity is reached leads to three straightforward and testable predictions. The first prediction focuses on the difference between mammals and birds. In contrast to mammals, birds not only complete their physical growth early in their development (and are therefore unlikely to be limited in the timing of maturity by energetic constraints) but also generally live in a skill-intensive foraging niche relative to mammals (Clutton-Brock, 2009). We expect the ASC/AFR ratio to be around 1 in most birds, whereas ASC/AFR should necessarily be less, and usually far less, than 1 in most mammals (prediction 1).

The second prediction concerns the relation between the ASC/AFR ratio and the complexity of the feeding niche among mammals. If prediction 1 is supported empirically, there will be a time gap between ASC and AFR in most mammals. We expect that those species that need to learn more skills would take longer to reach ASC, so their ASC/AFR ratio should eventually approach 1. Thus, we predict an increase in the ASC/AFR ratio with increasing skill intensity of the niche (prediction 2).

The third prediction concerns the possible conditions allowing evolutionary increases in the ASC/AFR ratio, i.e. the evolution of a more complex foraging niche. We predict that in mammals, a species can afford to reach ASC after weaning when juveniles have an energetic buffer against potential energy deficits caused by failures during periods of learning, which allows some learning to take place after weaning. Thus, prediction 3a is that increased ASC/AFR has historically been achieved in two basic conditions that reduce the impact of learning failure: slow conservative development and post-weaning provisioning.

Prediction 3b focuses on how it is possible to delay skill competence until *after* age at first reproduction, as seen in humans. If this is accompanied by a skill intense feeding niche, we can attribute the value of ASC/AFR >1 to increase of ASC rather than reduction of AFR. We propose that the only way individuals can start reproducing before they have reached adult-level foraging skill competence is when harvested resources are pooled and shared among all group members, which is only expected in (some) cooperative hunters.

So far, no systematic comparative test of these predictions has been undertaken. Here, we collected literature data on skill ontogeny of different mammal and bird species to test them. In this, as in previous studies (Kaplan et al., 2000), the development of foraging skills was used as a measure of skill competence.

Material and Methods

We compiled a dataset on the development of foraging skills and age of first reproduction of 23 bird and 34 mammal species (13 primates, 13 carnivores, 5 ungulates, 2 bats, and 1 cetacean, see appendix). Data on age of first reproduction were taken from an established database (K. Isler, unpublished data). We focused on female age at first reproduction only as this is more easily definable. Data on the development of foraging skills was retrieved from published studies.

For each species, an ASC/AFR ratio was calculated by dividing age at skill competence by age at first reproduction. As age at skill competence we took the youngest reported age (or the average age of the youngest age class respectively) that showed no difference in the measured foraging skill to adult (i.e. breeding) conspecifics. The accuracy at which the age of skill competence could be determined varied from study to study depending on how precisely the increase in skills was described (e.g. how broadly age groups were defined). Measures of foraging competence varied for the different species because studies varied in detail: whenever possible, data on foraging efficiency, intake rate and capture rate were used as these measures allow for a precise assessment of when adult like skills are reached. However in some studies only general data on mastery of foraging skills or diet composition were available. Accordingly, measures of foraging competence were divided into “strong” and “weak” predictors of the actual competence level (Table 1). All statistical analyses were therefore performed on two data sets (see appendix): an unrestricted analysis including all mammal species (n=34) and a restricted, more conservative analysis to assure data quality (n=18). The restricted analysis (i) included only taxa for which “strong” measures of skill competence was available (Table 1), (ii) excluded species for which the age at skill competence could only be broadly defined, and (iii) excluded taxa where the increase in foraging proficiency was likely due to increase in size or strength rather than skills. Graphs generally represent the unrestricted analysis, showing 34 mammal species.

For the bird-mammal comparison, three categories of skill development trajectories were defined: (1) adult level of skills is reached *before AFR*: before 85% of the developmental period is completed, (2) adult levels of skills is reached *around AFR*: after 85% and before 115% of the developmental period is completed, and (3) highest values in skills are reached *after AFR*: after 115% of the developmental period is completed.

According to their breeding and foraging system, mammal species were divided into solitary breeders and cooperative breeders, and also in independent foragers and cooperative hunters. Mammal species were also divided into four niche-complexity categories according to the level of processing needed during food acquisition. Largely following Kaplan et al. (2000), category 1 represents the lowest, and category 4 the highest niche complexity (Table 2). All analyses were done in R 2.13.1 (R Development Core Team, 2011) and BayesTraits (available on <http://www.evolution.reading.ac.uk>). To

correct for the impact of phylogenetic non-independence, phylogenetic generalized least square (PGLS) regression was used in the R package *caper* (Orme et al., 2011). All graphs are meant for illustrative purposes only, because the significance is always based on the complete statistical models.

Results

The first prediction concerned the broad bird-mammal difference. Among birds, 20 of the 23 species have ASC/AFR of around 1, i.e. reached adult level of foraging competence around the age of first reproduction. All but two (which were cooperative breeders) of the bird species included in the analysis were pair-breeding. In 24 of the 34 mammal species, adult levels of foraging skill competence are reached well before AFR, in eight around AFR, and in two after AFR (Fig. 3). To obtain a phylogenetically informed modal value of the relative age at skill competence in the two radiations, we calculated the ancestral state of the ASC/AFR value for birds and mammals separately by using GLS in *BayesTraits* (Pagel, 1997; Nunn, 2011). The ancestral ACS/AFR value of birds was estimated to be 0.98 ± 0.034 (SD), the one of mammals to be 0.68 ± 0.01 (SD).

The second prediction was that the complexity of the foraging niche should reflect the age at which adult skill level is reached in mammals. As predicted, a PGLS regression showed that the ASC/AFR ratio was positively correlated with niche complexity (Table 3). Thus, as the feeding niche becomes more complex, maturing mammals need more time to learn their foraging skills (Fig. 4).

The third prediction concerned possible conditions in which the ASC/AFR ratio can be increased by selection. First of all (prediction 3a), we predicted that skill competence should be reached later in development when there is post-weaning provisioning or the species shows a slow, conservative development. A PGLS model showed that both post-weaning provisioning and the pace of development have a significant positive effect on the relative age of skill competence. In the statistical model $\ln(\text{ASC})$ was used as response variable, and post-weaning provisioning and development pace as factors. Due to the high correlation between age at first reproduction (AFR) and body mass, we included both relative AFR (the residual AFR vs. body mass) as a proxy of development pace and body mass itself as factors. The model itself was highly significant and so were all effects (Table 3, Fig. 5A and 5B). Thus, adult-level skills are reached later in mammals that have slow development for their body size or that show post-weaning provisioning.

Prediction 3b focused on how ASC can be reached after AFR, in other words, how ASC/AFR can become >1 . We predicted that this is only possible if there is intensive food sharing among adult individuals. Consistent with our prediction, we found that cooperatively hunting species reach skill competence significantly later than independently foraging species (Table 3, Fig. 6). Indeed, all

cooperatively hunting species in the sample had ASC/AFR ratios between 1 and 2.38 whereas all other independently breeding species showed values less than 1.

Discussion

Time to grow or time to learn?

In this study, we asked for both birds and mammals whether time at sexual maturity (age at first reproduction, or AFR) is determined by the time when adult body size is reached or when adult-level foraging skills (ASC) are reached, in order to explain the unusually late ASC in humans. We therefore looked at whether energy supply (somatic growth and development) or time to learn vital skills is limiting the duration of the immature period. We predicted a major difference between birds and mammals. Indeed, we found that birds, which reach adult body size very early, reach maturity, i.e. begin breeding, around the time they reach adult-level foraging skills. This confirms that among birds time needed to learn skills is indeed limiting the period of immaturity, and reflects the exceptionally high initial rates of growth and parental investment in altricial birds (Lack, 1968).

In contrast, we found that most mammals reach adult skill levels well before reaching maturity, confirming the traditional view that the immature phase among mammals is best explained by classic life-history theory combined with the notion that the high energy costs of the brain further slow down overall physical development. Thus, time needed to learn skills does not determine age at first reproduction among mammals in general, most likely because most newly weaned mammals must have the skills to be self-supporting, yet still have much growing to do, being only approximately one third of adult body size (Lee, 1997). Because failures during periods of learning may have severe consequences for growing organisms (as they lead to lower food intake and consequently carry the risk of brain starvation: Isler and van Schaik, 2009a), it is very likely that many species have reached skill competence by the age of weaning.

Among mammals, there is nonetheless much variation in the age at which adult skill competence (ASC) is reached relative to the age at first reproduction (AFR). We found that this variation was related to the complexity of the species' foraging niche. As this complexity increases, adult-level foraging skills are reached later, indicating that living in a complex niche requires learning over a relatively longer time span. The analysis thus clearly showed that some mammal species have found ways to prolong the period of learning until long after the age of weaning. The modal value of mammal's ASC/AFR, controlled for phylogenetic relatedness, was estimated as 0.68. This may seem high, but it is likely that this value is biased because our data set included a disproportionately high number of species living in rather complex niches (primates, carnivores) and only a few of the many species that live in

1 simple niches (such as ungulates or rodents). This publication bias probably exists because studies of
2 skill learning are not considered interesting in species with simple foraging niches.

3 The next step was to look at the actual mechanisms that allow for learning after weaning and
4 therefore allowed species to evolve into a complex niche. We could envision three conditions in which
5 the age of adult-level skill competence can be delayed towards age of first reproduction (Fig. 7). The first
6 condition may be most common but quantitatively least important, because it favors only the diet
7 choice part of the ecological skills rather than food finding and processing. Stable gregariousness allows
8 juveniles to continue to associate with adults post-weaning, enabling them to follow knowledgeable
9 adults to food sources they might not have discovered on their own. Such copying of diet choices may
10 account for some of the variation in our data set: especially in group-living primates skill competence
11 does not necessarily have to be reached right at the age of weaning even though there is no post-
12 weaning provisioning.

13 The second condition, exemplified by the great apes or capuchin monkeys, is where due to very
14 low rates of unavoidable mortality, physical growth has become so slow, perhaps because selection
15 favors conservative growth rates (Janson and van Schaik, 1993), that reduced food intake rates due to
16 imperfect skills do not endanger survival. Thus, enough time is created under normal (non-starvation)
17 conditions to learn many skills. Among Sumatran orangutans, for example, which are weaned at around
18 age 8, adult skill levels are reached around age 12, which is well after weaning but still well before they
19 start to breed, around age 15.5 (van Noordwijk et al., 2009; Schuppli, 2012).

20 The third condition is post-weaning provisioning, which buffers against lack of foraging
21 competence and thus risk of occasional starvation of incompetent foragers, and consequently allows
22 them to learn complex foraging skills. In these species, the ASC/AFR ratio can approach 1, which allows
23 species to inhabit more complex niches, although this is obviously not inevitable.

24 The final step is the explanation of the fact that in some species ASC is reached well after the
25 onset of reproduction (AFR). In addition to humans, we found that ASC/AFR consistently exceeded 1 in
26 cooperative hunters, with values ranging from 1 and 2.38. This supports the hypothesis that a
27 cooperative hunting system is associated with very late ASC. Thus, systematic food sharing among adults
28 due to cooperative hunting may be the key variable to explain this unexpected phenomenon: Individuals
29 don't have to exhibit full hunting proficiency to be successful adults and reproduce.

30 Skill learning and human evolution

31 Having gained this overview of the factors determining ASC relative AFR in mammals, we can
32 return to the unusually late ASC in humans. Humans combine all three possible causes for late ASC.
33 Humans do not just show the gregariousness and slow development inherited from our great ape
34 ancestor, but modern foragers are also cooperative breeders and hunters, with both intense

provisioning of juveniles and obligate sharing of all harvested and hunted food among adult individuals (Gurven et al., 2006). Therefore, in contrast to great apes and most other primate species, but as in other cooperatively hunting carnivores, human foragers can afford to reach adult-level foraging skills well after the onset of reproduction. Furthermore, humans show a cooperative breeding system with extensive support of the breeders from other group members. All this strongly suggests that the complexity of the human foraging niche, and our great intellectual ability and unusually large brain size in general, coevolved with the combination of food sharing and provisioning (Hrdy, 2009; Burkart et al., 2009), which developed on top of a great ape-like life history. We have suggested elsewhere that this life style began relatively early in human evolution, with the emergence of *Homo erectus* (van Schaik and Burkart, 2010; Isler and van Schaik, in press). Thus, cooperative breeding and hunting enabled the gradual increase in the complexity of our foraging niche, and thus our brain size.

These results help to place the embodied capital hypothesis (Kaplan et al. 2000, 2007) into a broader context, by suggesting that this hypothesis, developed specifically to explain the human condition, combines two distinct elements that can be seen as broadly independent biological processes: (i) the coevolution between brain size and life history, including both development time and total lifespan, and (ii) intergenerational transfers.

In the form it is generally presented (e.g. Kaplan and Robson, 2002), the first element provides an alternative but equivalent formulation of the basic life-history explanation for brain-life history coevolution (cf. Deaner et al., 2003). This coevolution can be explained with reference to the costs of growing a larger brain (Isler & van Schaik, 2009a; Navarrete et al., 2011), which thus leads to delayed maturation. However, this only produces a viable demography in species that have a sufficiently increased adult lifespan (due to the survival benefits bought by the larger brain). The nature of these development costs is not specified in this hypothesis: both a slowdown of overall somatic growth and an increase in time needed to acquire the necessary skills can produce the same correlation between brain size and life history.

This first element is effective, but on its own falls short in explaining why humans are so extreme in both brain size and longevity relative to all other mammals. The reason that mammals are limited in how far these two variables can be increased is that they hit a gray ceiling (Isler and van Schaik, 2009b; 2012). At the highest skill levels, and thus probably the largest brain sizes, the delay in AFR increases, and as we noted, this is increasingly due to the time needed to learn vital skills. The delay in AFR is counteracted by the increase in adult lifespan, but this compensation is increasingly inadequate as brain size increases because the increase in lifespan is limited due to unavoidable mortality, and in addition birth rates generally go down rather than up with increasing brain size (Isler and van Schaik, 2009b). Demographic non-viability would therefore result if brain size were to increase any further. Brains and

maximum lifespan therefore remain stuck at some moderate level: the gray ceiling. In great apes, for instance, brains are roughly one third of those of humans and lifespan roughly two decades less (Robson et al., 2006).

The second element, intergenerational transfers, is therefore critical to explain how hominins broke through this gray ceiling. In mammals in general, allomaternal inputs increase the reproductive output of adults to improve demographic viability, and thus allow the gray ceiling to be moved up: cooperative breeders have larger brains than their independently breeding relatives (Isler and van Schaik, 2012). However, this process will still continue to be limited by the constraint that ASC cannot exceed AFR. This is where the intergenerational transfers come in: they allow $ASC > AFR$, and thus continuing evolution of more complex niches. The only other organisms in which intergenerational transfers are seen are cooperative hunters, which share widely. Thus, the combination of immature provisioning and continued food sharing in hominins allowed brains to increase well beyond the relative size seen in other mammals. In addition, intergenerational transfers further improve survival of both immatures and adults (because it involves sharing among adults as well), which in turn enables the evolution of even longer lifespan (Gurven et al., 2012). Finally, as skills became more complex, adult productivity increased to levels well beyond what is necessary, thus making the transfers possible and sustaining the coevolutionary cycle.

Conclusion

In sum, the human lifestyle with the complex foraging niche is made possible by two processes: (i) the mammal-wide correlated evolution between brain size and life history and (ii) the intergenerational resource transfers made possible by cooperative breeding and hunting (Hill & Kaplan, 1999; Kaplan et al., 2000). By adding intergenerational food transfers to a system of relatively complex foraging niches (extractive foraging, some cooperative hunting), hominins could make the niche more complex and allow learning times to exceed the time needed to reach sexual maturity.

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15

1 **Tables:**
2 **Table 1.** Validity of the different measures of foraging competence in mammals.

Validity of measure	Measure of foraging competence
Strong	intake rate
	capture rate
	processing rate
	handling time
Weak	diet composition
	feeding time
	mastery of foraging techniques

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Table 2. Niche complexity categories in mammals based on level of processing needed for food acquisition.

Niche complexity	Species	Level of processing
1	Folivores and grazers	No processing
2	Frugivores and insectivores	Low-level processing
3	Extractive foragers and mobile prey catchers	High-level processing
4	Big game hunters	High-level processing and risk

Table 3. Summary of the PGLS regression models used to test the different predictions about the effects of different factors on age of skill competence (ln(ASC)) in mammals. Effects are shown in bold face, the other variables are covariates used to control for body size effects. A) unrestricted (N=34) and B) restricted dataset (N=18).

A) unrestricted dataset (N=34 species)

Prediction	P-value of model	R ²	F-statistic	Lambda	Effects	P-value of effects	Effect size β
2	< 0.001	0.51	17.9	0.54	Niche complexity	0.001	0.46
					ln(AFR)	<0.001	0.92
3a	< 0.001	0.52	12.76	0.38	Residual AFR	<0.001	1.03
					Provisioning	0.035	0.64
					ln(body mass)	<0.001	0.19
3b	< 0.001	0.52	12.89	0.52	Cooperative hunting	0.007	1.07
					ln(AFR)	<0.001	1.07

B) restricted dataset (N=18 species)

Prediction	P-value of model	R ²	F-statistic	Lambda	Effects	P-value of effects	Effect size β
2	0.002	0.45	8.08	0.55	Niche complexity	0.057	0.52
					ln(AFR)	0.013	0.96
3a	< 0.001	0.68	12.98	0.99	Residual AFR	0.032	0.91
					Provisioning	<0.001	1.82
					ln(body mass)	0.009	0.21
3b	< 0.001	0.72	22.4	0	Cooperative hunting	0.004	1.78
					ln(AFR)	<0.001	1.38

Figure Legends

Fig. 1. Age at first reproduction (AFR) versus brain size in mammals and birds, depicting non-phylogenetic least-squares regression lines. Humans were not included in the calculations, but are shown for comparison. The analysis was phylogenetic multiple least-squares regression (PGLS) with \ln AFR as response variable, \ln brain size and \ln female body mass as effects: A) precocial mammals (N=301 species, brain: $\beta=0.26$, $p<0.001$, body: $\beta=0.03$, $p=0.542$); B) altricial mammals (N=312, brain: $\beta=0.25$, $p=0.030$, body: $\beta=0.05$, $p=0.506$); C) precocial, semiprecocial and semialtricial birds (N=419, brain: $\beta=0.25$, $p=0.008$, body: $\beta=0.13$, $p=0.018$); D) altricial birds (N=392, brain: $\beta=0.21$, $p=0.019$, body: $\beta=0.09$, $p=0.143$).

Fig. 2. Both energetic tradeoffs and the time to learn skills have the potential to influence the length of the immature period. As soon as both adult-level skills and adult body size are reached, successful reproduction is possible. AFR= age of first reproduction, ASC= age of skill competence, E= pace of development, S= rate of skill acquisition. A) Time to acquire adult skill level determines age at onset of reproduction. B) Energy to reach adult body constitution determines age at onset of reproduction. C) Highest skill levels are reached after onset of reproduction.

Fig. 3. Distribution of the different classes of skill development in mammals and birds.

Fig. 4. Relative age at skill competence as a function of niche complexity in mammals. Values above the dashed line mean that full skill competence is reached after AFR.

Fig. 5. (a) Relative age at skill competence of mammal species without post-weaning provisioning versus mammal species with post weaning provisioning. (b) Relative age at skill competence as a function of residuals AFR (as measure of the pace of development) for mammal species without post-weaning provisioning and mammal species with post-weaning provisioning.

Fig. 6. Relative age at skill competence of independently foraging versus cooperatively hunting mammal species.

Fig. 7. Evolutionary pathways that enable the evolution into a skill-intensive foraging niche.

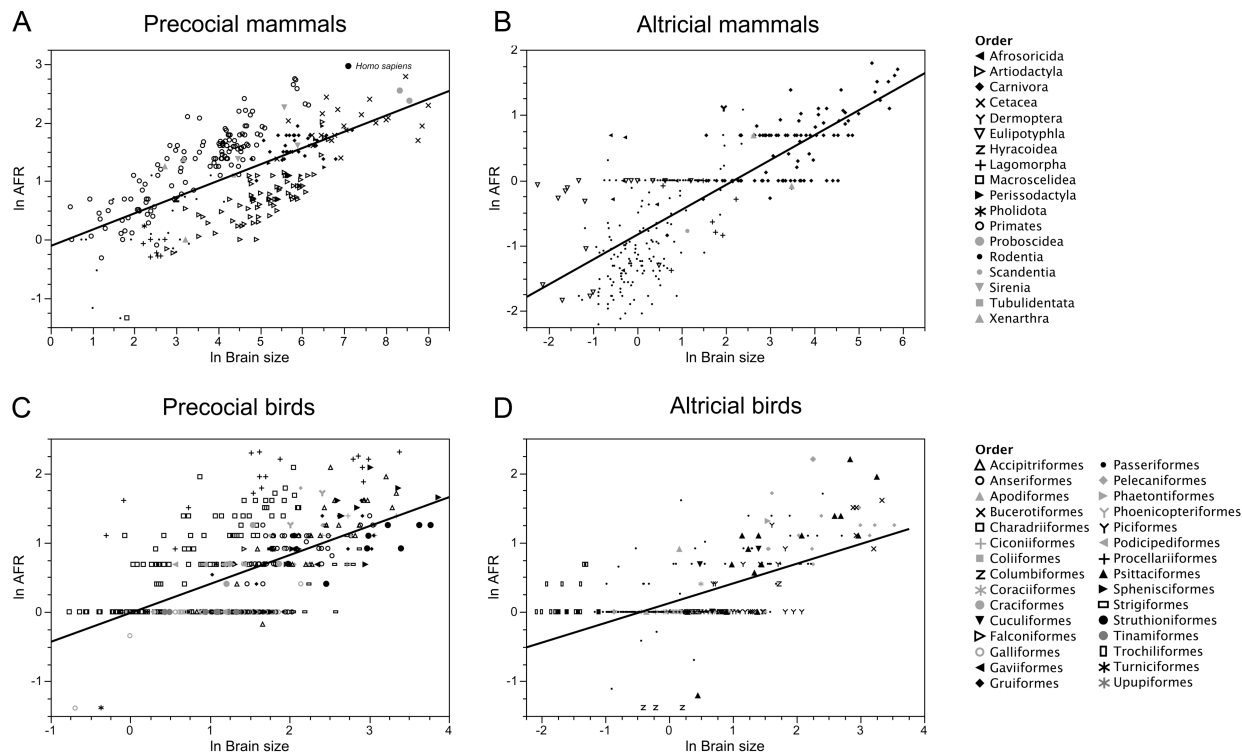


Figure 1

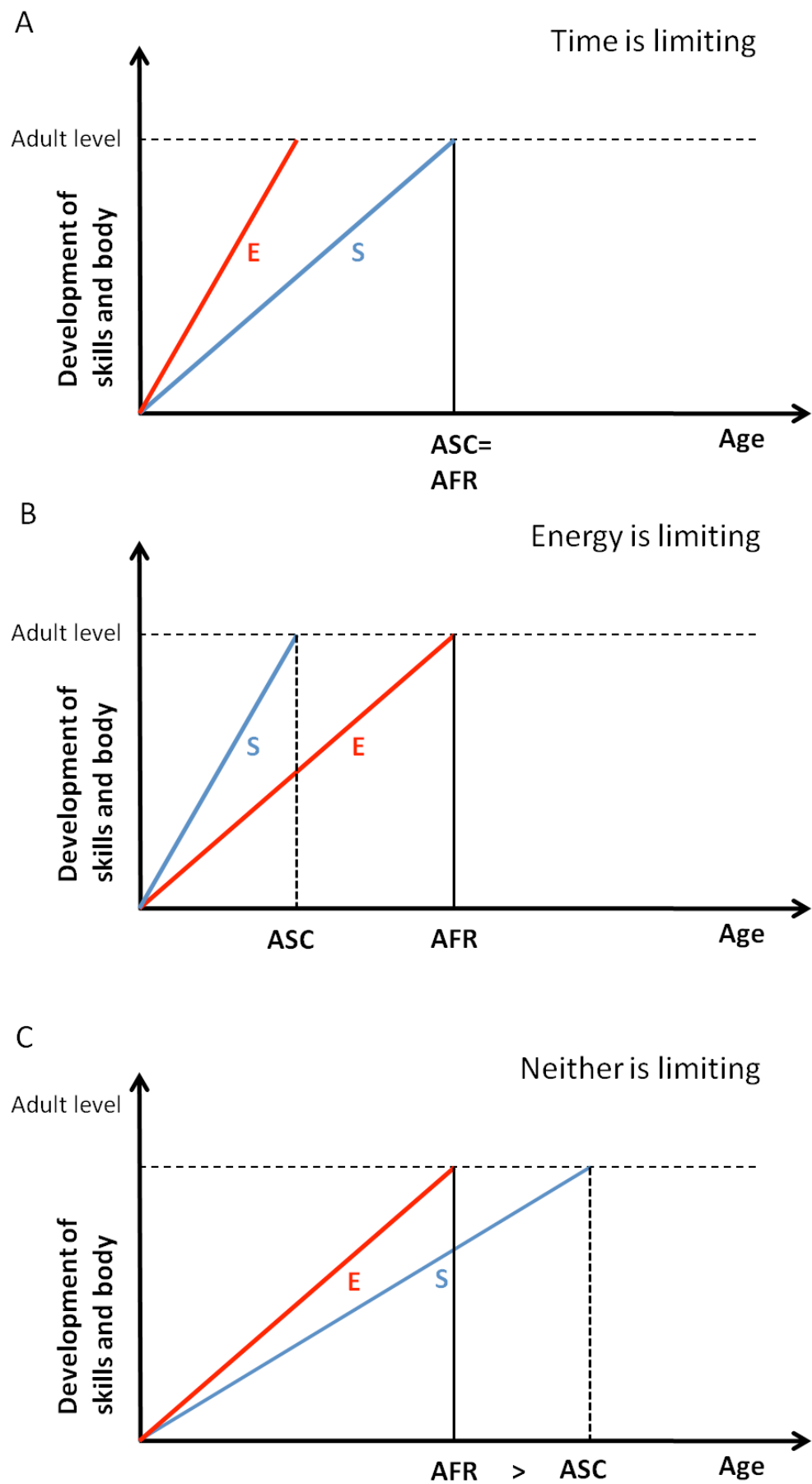


Figure 2

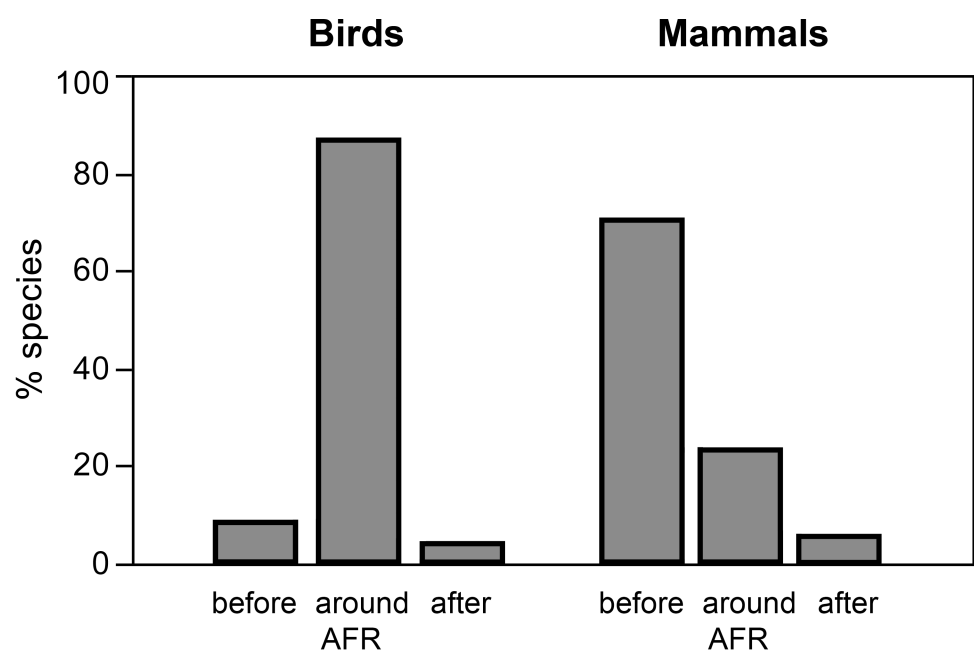


Figure 3

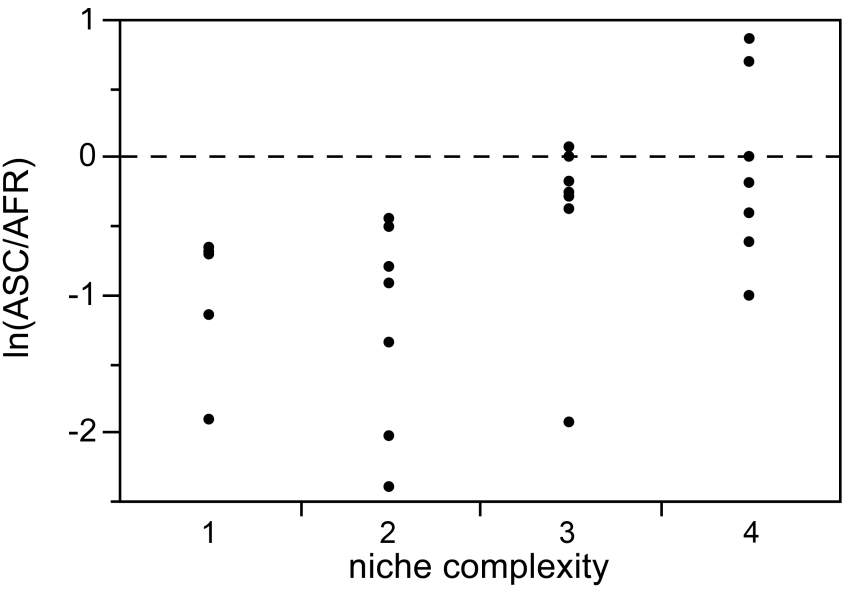


Figure 4

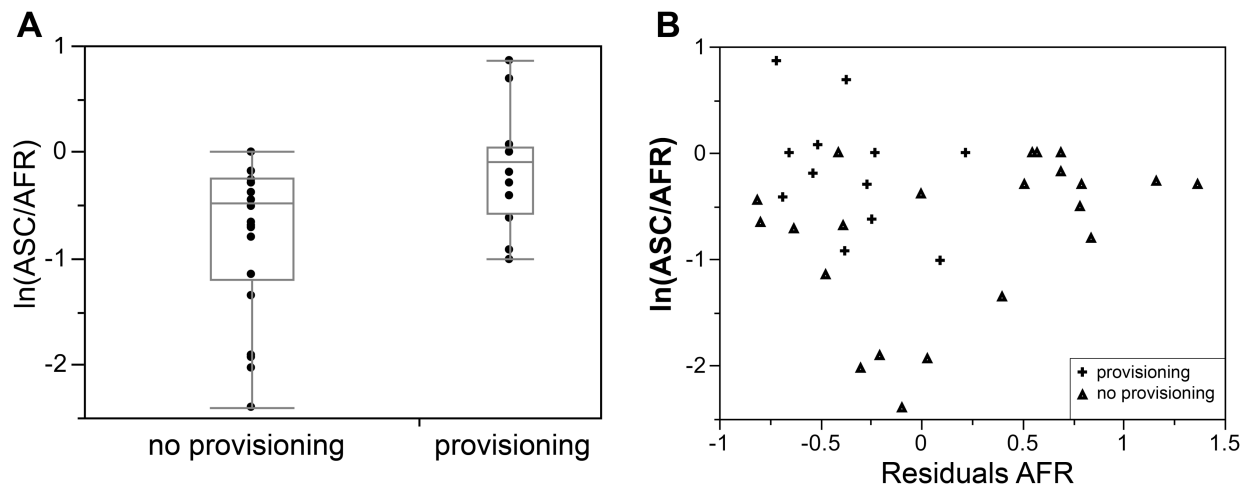


Figure 5

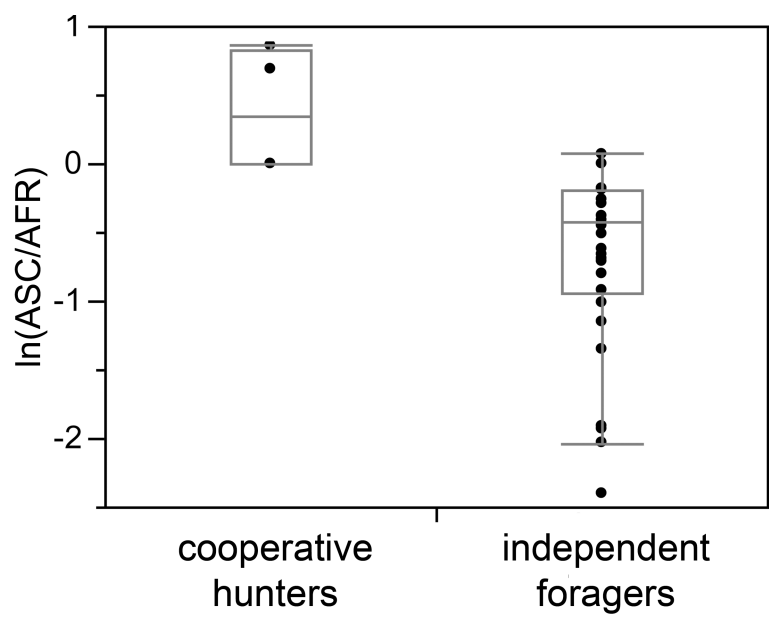
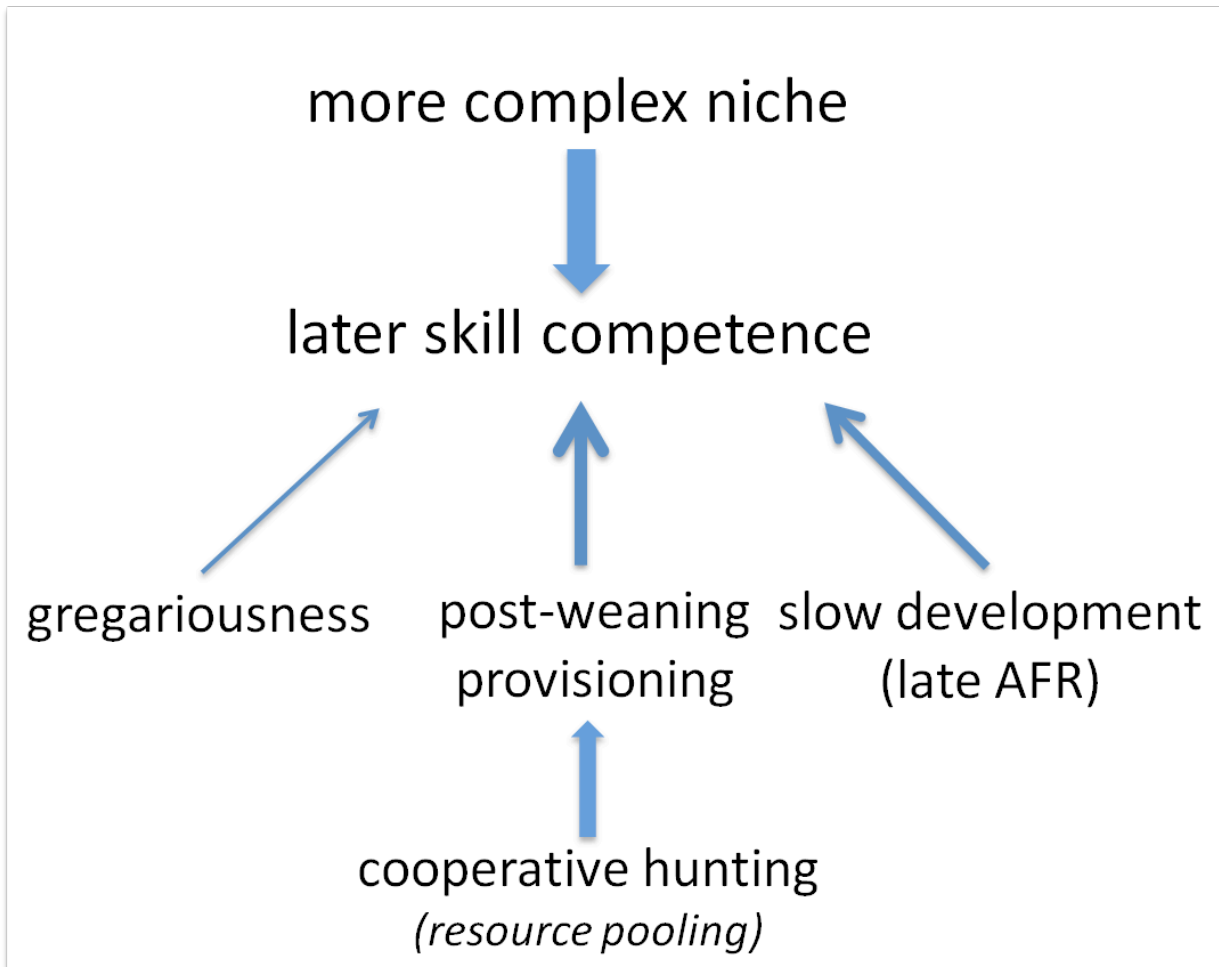


Figure 6



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Figure 7

Appendix

Table A1: Mammal data including adult female body mass, AFR (age at first reproduction in females), niche complexity (as defined in Table 2), post-weaning provisioning, cooperative hunting, ASC/AFR ratio (age at first reproduction divided by age at skill competence), classification of the measure of foraging competence (see Table 1) and whether the data was used in the unrestricted analysis only (U) or also in the restricted analysis (U&R, based on the criteria described in the Methods).

Species	female body mass [kg]	AFR [y]	niche com- plexity	post- weaning provisio- ning	coope- rative hunting	ASC/AFR ratio	measure of compe- tence	Ana- lysis	References
Cetartiodactyla									
<i>Cervus nippon</i>	20.1	2	1	0	0	0.49	weak	U	Koga and Ono 1994
<i>Giraffa camelopardalis</i>	828	4.8	1	0	0	0.15	weak	U	Ciofolo and Pendu 2002
<i>Odocoileus hemionus</i>	55.7	1.9	1	0	0	0.52	strong	U&R	Gillingham et al. 1997 Oakes and Harmsen 1991;
<i>Ovibos moschatus</i>	250	3.2	1	0	0	0.32	weak	U	Forchhammer 1995
<i>Ovis canadensis</i>	72	3	1	0	0	0.5	strong	U&R	Ruckstuhl et al. 2003
<i>Tursiops truncatus</i>	172	5.5	3	1	1	1	weak	U	Sargeant et al. 2005
Carnivora									
<i>Acinonyx jubatus</i>	43	2.1	4	1	0	0.67	weak	U	Eaton 1970; Schaller 1967 MacNulty et al. 2009a,b; Sand et al.
<i>Canis lupus</i>	38.5	2	4	1	1	2.38	strong	U&R	2006
<i>Crocuta crocuta</i>	64.8	3	4	1	1	2	strong	U&R	Holekamp et al. 1997
<i>Enhydra lutris</i>	23.5	4	3	0	0	0.15	strong	U&R	Payne and Jameson 1984
<i>Helogale parvula</i>	0.265	1.4	3	1	0	1.07	strong	U&R	Rasa 1972
<i>Lutra lutra</i>	6.75	2.7	3	1	0	1	strong	U&R	Heggberget and Moseld 1994
<i>Lycaon pictus</i>	22.05	2	4	1	1	1	weak	U	Malcom and Marten 1982; Estes 1967 Maehr and Brady 1986; McLean et al.
<i>Lynx rufus</i>	7.5	2	4	1	0	0.83	weak	U	2005; Fritts and Sealander 1978
<i>Meles meles</i>	10.1	1.6	2	0	0	0.64	weak	U	Roper and Lups 1988
<i>Mirounga leonina</i>	503	3.6	3	0	0	1	weak	U	Field et al. 2006
<i>Panthera tigris</i>	130	3.7	4	1	0	0.54	weak	U	Seidensticker 1993; Schaller 1967
<i>Suricata suricatta</i>	0.72	2	3	1	0	0.75	strong	U	Clutton-Brock 2006; Thornton 2008
<i>Ursus maritimus</i>	225	5.5	4	1	0	0.36	strong	U&R	Stirling and Latour 1977
Chiroptera									
<i>Myotis velifer</i>	0.009	1.2	2	0	0	0.13	strong	U&R	Kunz 1974
<i>Pipistrellus pipistrellus</i>	0.006	1.4	2	0	0	0.09	strong	U&R	Swift 1981
Primates									
<i>Callithrix jacchus</i>	0.381	1.7	2	1	0	0.4	strong	U	Schiel et al. 2010
<i>Cebus apella</i>	2.52	6.7	3	0	0	0.75	strong	U&R	Gunst et al. 2008; Gunst et al. 2010
<i>Cebus capucinus</i>	2.54	6	3	0	0	1	strong	U	O'Malley and Fedigan 2005
<i>Cebus olivaceus</i>	2.52	6	3	0	0	0.83	strong	U&R	Fragaszy and Boinski 1995
<i>Gorilla beringei</i>	97.5	10	2	0	0	0.6	strong	U&R	Watts 1985; Watts 1988
<i>Gorilla gorilla</i>	71.5	10.2	2	0	0	0.45	strong	U&R	Nowel and Fletcher 2007
<i>Macaca fuscata</i>	8.03	6.1	3	0	0	1	strong	U	Nakayama et al. 1999; Hanya 2003
<i>Papio cynocephalus</i>	12.3	6	3	0	0	0.75	strong	U	Post et al. 1980
<i>Papio hamadryas</i>	9.9	6.1	3	0	0	1	strong	U	Johnson and Bock 2004
<i>Papio ursinus</i>	14.8	3.7	3	0	0	0.68	strong	U&R	Byre et al. 1992
<i>Pongo abelii</i>	35.8	15.5	3	0	0	0.77	strong	U&R	Schuppli 2012
<i>Pongo pygmaeus</i>	35.6	13	3	0	0	0.83	strong	U&R	Dunkel 2006
<i>Saimiri sciureus</i>	0.662	3.9	2	0	0	0.26	strong	U&R	Stone 2005

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